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Species Lifetime Distribution for Simple Models of Ecologies

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Abstract

Interpretation of empirical results based on a taxa's lifetime distribution shows apparently conflicting results. Species' lifetime is reported to be exponentially distributed, whereas higher order taxa, such as families or genera, follow a broader distribution, compatible with power law decay. We show that both these evidences are consistent with a simple evolutionary model that does not require specific assumptions on species interaction. The model provides a zero-order description of the dynamics of ecological communities and its species lifetime distribution can be computed exactly. Different behaviors are found: an initial $t^{-3/2}$ power law, emerging from a random walk type of dynamics, which crosses over to a steeper t^{-2} branching process-like regime and finally is cutoff by an exponential decay which becomes weaker and weaker as the total population increases. Sampling effects can also be taken into account and shown to be relevant: if species in the fossil record were sampled according to the Fisher log-series distribution, lifetime should be distributed according to a t^{-1} power law. Such variability of behaviors in a simple model, combined with the scarcity of data available, cast serious doubts on the possibility to validate theories of evolution on the basis of species lifetime data.

Introduction

Ecosystems have become paradigmatic examples of complex systems, showing organization and collective dynamics across very different time and spatial scales [1]. These features are captured by non trivial relationships among measurable quantities, which take forms familiar to statistical physics. Well known examples include the species-area scaling relationship [2,3], allometric relations [4–7], and the occurrence of power laws in the distributions of species lifetime and size of extinction events [8–10]. These statistical laws have been measured over many orders of magnitude and exhibit similar patterns across very different living ecosystems and also in different quantitative studies of fossil records [11]. The ubiquity of these patterns [12] suggests that they may be amenable to be studied in a general and a-specific framework.

In this article, we will address the issue of species (or more general taxa) lifetime distribution. Although the analysis of fossil records has recently highlighted several

patterns in the evolution of biodiversity, and motivated the proposition of different mechanisms that may have caused these patterns, the functional form of the species lifetime distribution remains a debated issue. According to several studies [13], species lifetime seems to be exponentially distributed. Others have found evidences of power law behavior with exponent close to -2 if genera, and therefore longer time scales, are considered ([12], see also [11] and reference therein). Keitt and Stanley [14] analyzed data sets from the *North American breeding bird survey* (<http://www.mbr.nbs.gov>) finding a power law distribution for species lifetime (in their study defined as the time between colonization and local extinction) with an exponent close to $-3/2$. In fact, the detailed analysis of Newman *et al.* [15] of the data by Raup [16] has shown how both these hypothesis consistently fit the data and, when a power law fit is applied, an exponent between $-3/2$ and -2 is estimated.

On the theoretical side, these different, not to say contrasting, findings have been invoked to support different macro-ecological theories. The power law behavior with exponent -2 is to be expected when species dynamics can be regarded as a critical branching process [17] where two or more species can originate at a random moment from a common ancestor and, also randomly, get extinct. An exponential behavior in the lifetime distribution is often referred to as Van Valen's law [18]. The mechanism proposed by Van Valen in support of this view is commonly known as the Red Queen effect: there may be no time enough for a species to gain evolutionary advantage over competing species before the rapidly changing environment completely re-draws the fitness landscape. As a consequence, the extinction probability of any species does not depend on time and an exponential behavior for lifetimes distribution easily follows. Several data sets support these conclusions [19–22] (see also [23] for further analysis of the same data). More recently, the occurrence of power law distributions with non trivial exponents has attracted particular attention, because of an ongoing debate on whether the observed patterns are caused by a self-organized critical dynamics [8–10] that would naturally lead to the notion of punctuated equilibrium [24]. In this framework an ecosystem is depicted as a system of interacting species whose dynamics converges spontaneously close to a critical point [12]: the extinction of a given species may trigger a cascade of extinction events starting from the species that depend upon, or directly interact with, the species just extinct and leading to fluctuations of any size in the number of extinction occurrences that may

contiguously take place.

The aim of the present paper is to show that all the behaviors mentioned above for the lifetime distribution are captured by a simple model of non-interacting species. We conclude, therefore, that it may be problematic, if not inappropriate to discriminate between existing macroecological theories on the basis of existent datasets. The framework we adopt here is inspired by the ecological neutral theory proposed by Hubbell [25] and thereafter extended and analytically studied in [26–30]. This class of models assumes that individuals in an ecological community are fully equivalent and the population of a species is essentially subject to a birth and death process. Then, each species undergoes the same dynamics: the reproductive success of each individuals depends only on the species population size, and not on the particular species considered. Competition among species is taken into account explicitly only via a constraint on the total population of the community and implicitly through averages birth and death rates.

From the point of view of evolutionary theory, the hypothesis of species equivalence may be still justified by a Red Queen effect [18], which is able to forbid the acquisition of a large evolutionary advantage (i.e. a significantly higher fitness level) of a species over its competitors. In the framework of population dynamics, this hypothesis implies that demographic stochasticity is the main driving force for the assembly of ecological communities, meaning that its effect is overwhelmingly strong compared to that of fitness differences among species, which, although present, may be neglected. It is worthwhile to stress that, in principle, complex ecological mechanism acting on long timescales are not ruled out by these stochastic models, as far as they can be included in effective birth and death rates. This consideration opens the issue of determining whether these theories are able to assess realistic predictions on large time and geographical scales, such as those relevant for the fossils observations. It is widely believed [1] that statistical physics may provide the tools to bridge these very different scales. In this perspective, it is encouraging that Conette *et al.*, [31] basing on the studies of the biodiversity time series compiled by Sepkosky and coworkers [32], recently concluded that a random walk-like model is not inconsistent with the observed biodiversity time-patterns.

The model we consider here is amenable to be analytically solved and is introduced in

the next section. The resulting lifetime distribution interpolates, through a scaling function, between the behaviors of two well known stochastic processes: exit time problem for the one dimensional random walk [33] and the critical Galton-Watson branching process [17]. Our results show that, even in a simple model in which interactions among species are included only in an averaged way, a variety of different behaviors for the distribution of extinction time is possible. In particular, depending on the relevant time-scales, we find an exponential, or a power law behavior. The latter can either occur with exponent -2 , typical of branching processes [17], or, for shorter time-scales, with a random walk like exponent $-3/2$. In addition, if we assume that the abundance of species is distributed according to a Fisher log-series [34], in the Galton-Watson case, we find a power law distribution of extinction times with exponent -1 .

As we will discuss in the conclusion, these results stress the importance of time-scales and sampling effects in the analysis of lifetime distributions. This theory, also, can easily accommodate the contrasting empirical observations of Refs. [11–13, 15] by assuming that, while species lifetimes probe the exponential regime of the theory, genera lifetimes fall in the power law range. The fact that power laws arise in an “effective” single-species theory, combined with the sparseness of available empirical data, suggests that it may not be possible to validate (or discard) ecological or evolutionary mechanisms like self-organized critical dynamics [12] on the basis of an observed non-exponential behavior in the lifetime distributions.

Description of the model

According to the assumption of neutrality [25, 26], the dynamics of our model is uniquely specified by the effective birth and death rates $b^{(n)}$ and $d^{(n)}$ that depend exclusively on the population size n .

We refer to the functions $b^{(n)}$ and $d^{(n)}$ as “effective” because they may embody, in a cumulative way, a variety of ecological causes that may, in principle, influence the increase/decrease over time of the number of individuals in a species, or, more generally, in a given taxon. The framework is therefore ample enough to describe

a population dynamics that is not simply dominated by demographic stochasticity, but also, for example, by immigration, emigration or niches assembly. We can safely assume that $b^{(n)}/n$ and $d^{(n)}/n$, the birth and death rates per individuals, can be expanded in a power series in $1/n$ around their asymptotic values b_1 and d_1 [28]:

$$\begin{aligned} b^{(n)}/n &= b_1 + b_0/n + b_{-1}/n^2 + \dots \\ d^{(n)}/n &= d_1 + d_0/n + d_{-1}/n^2 + \dots \end{aligned} \quad (1)$$

The non-zero coefficient in this Taylor series can be generally related to various kind of ecological effects giving advantages (or disadvantages) to a less abundant species with respect to a more abundant one. In Hubbell's theory [25, 26] the terms b_0 and d_0 maybe interpreted as the result of an immigration/emigration mechanism which couples the community to a meta-community living on a larger geographical scale. The mechanisms described by higher power in $1/n$ in Eq.(1) are relevant only for small population sizes and they are unable, reasonably, to affect properties observed on large spatial scales and long timescales. In the following, therefore, we will study the dynamics described only by the first two terms in the expansion of Eq. (1):

$$\begin{aligned} b^{(n)} &= b_0 + b_1 n \\ d^{(n)} &= d_0 + d_1 n \end{aligned} \quad (2)$$

for all $n \geq 1$. Despite the simple form of the birth and death rates, and the simplicity of the assumptions, this class of models is able to provide very good fits of species abundance relation [26–28] which can be related to the probability P_n of having species with population n . This probability, P_n , evolves with time according to a birth and death master equation:

$$\frac{d}{dt}P_n(t) = b^{(n-1)}P_{n-1}(t) + d^{(n+1)}P_{n+1}(t) - (d^{(n)} + b^{(n)})P_n(t) \quad (3)$$

We impose $b_1 < d_1$, ensuring that the average number of individuals is finite and there is no "demographic explosion". The ratio $\alpha \equiv b_1/d_1$ fixes, in-fact the average population per species [27, 28].

In order to study the lifetime distribution, we consider an absorbing barrier at $n = 0$, imposing $b^{(0)} = d^{(0)} = 0$. The initial condition is that the new species at time $t = 0$

has just one individual:

$$P_n(0) = \delta_{n,1} \quad (4)$$

Making these assumptions, $P_0(t)$ represents the probability of being already extinct at time t and the lifetime probability distribution function (or exit time distribution), $p(t)$, is just the time derivative of $P_0(t)$:

$$p(t) = \frac{d}{dt}P_0(t). \quad (5)$$

We will first examine the two limit cases $b_1 = d_1 = 0$ and $b_0 = d_0 = 0$, and then move to the general case.

Results

When $b_1 = d_1 = 0$ the number of individuals belonging to a given species undergoes a random walk in n space where b_0 (d_0) is the probability per unit time to jump one step to the right (left). A species lifetime would therefore correspond to the time it takes to the random walk to reach $n = 0$, i.e. to exit the positive axis. The problem of exit time distribution for a random walk process has been widely studied in the literature (see, for example, [33]). In particular, it is well known that in the critical case $b_0 = d_0$ the lifetime follow a distribution of the form $p(t) \sim t^{-3/2}$. Indeed it is easy to verify that the solution of Eq. (3), in the present case, is:

$$\begin{aligned} P_0(t) &= 1 - \exp(-2t)(I_0(2t) + I_1(2t)) \\ P_k(t) &= \exp(-2t)(I_{k-1}(2t) - I_{k+1}(2t)) \quad k > 0, \end{aligned} \quad (6)$$

where $I_k(z) = \frac{1}{\pi} \int_0^\pi \exp(z \cos(\theta)) \cos(k\theta) d\theta$ are modified Bessel functions of integer order and the unit of time has been chosen such that $b_0 = d_0 = 1$. Since for large z , $I_0(z) \propto e^z / \sqrt{z}$ from Eqs. (5) and (6) it follows that $p(t) \sim t^{-3/2}$ asymptotically.

Let us now analyze the case $b_0 = d_0 = 0$. This limiting case is interesting from an ecological point of view because the d_0 and b_0 terms happen to be small when one looks on a very large scale (like on continental scale). The dynamics is equivalent to a Galton-Watson process in continuous time [17]: the asymptotic behavior of the lifetime distribution is a classic result of the theory of critical branching processes [35].

Also in this case, the birth and death equation can be analytically solved: defining the characteristic function $G(x, t) = \sum_{n=0}^{\infty} P_n(t) x^n$ the birth and death equation can be transformed in a first-order p.d.e. for the function G , which can be integrated with the characteristics method. In the following, without loss of generality, we set $d_1 = 1$ and the initial condition in Eq. (4) translates in $G(x, 0) = x$. As shown in details in the Supplementary Material the exact solution is:

$$p(t) = \left(\frac{1 - \alpha}{e^{(1-\alpha)t} - \alpha} \right)^2 e^{(1-\alpha)t} \quad (7)$$

This distribution has an exponential-like shape when $(d_1 - b_1)$ (or $1 - \alpha$) is not too small. On the other hand, when b_1 approaches d_1 , the distribution has a power law behavior with exponent -2 and a characteristic timescale $t^* = \frac{1}{1-\alpha}$. The distribution $p(t)$ can be casted in a more appealing form by using the language of critical phenomena in statistical mechanics. For large t and t/t^* fixed, it follows, from Eq. (7), that:

$$p(t) = \frac{1}{t^2} f\left(\frac{t}{t^*}\right) \quad (8)$$

where $f(x) = [x/(1 - e^{-x})]^2 e^{-x}$. Thus plotting $t^2 p(t)$ versus t/t^* one get, in the scaling region, a universal curve where all the model details are absorbed in the characteristic time scale, t^* . When dealing with observational data, an estimate of t^* can be obtained by the ratio of two consecutive moments, $\langle t^k \rangle$ ($k \geq 1$), of lifetime p.d.f. .

It is also interesting to investigate the role of the initial condition on the lifetime p.d.f.. Taking into account an effective speciation rate, one can show, for the particular case at hand, that the resulting stationary distribution [26] is the celebrated Fisher log series [34]:

$$P_n = \mathcal{N} \frac{\alpha^n}{n} \quad (9)$$

where $n > 0$ and \mathcal{N} is a normalization constant. Using the result above it is therefore possible to calculate the expected extinction time of a species that is chosen at random in the ecosystem. Setting as initial conditions the characteristic function associated to the distribution (9), $G(x, 0) = \log(1 - x\alpha)/\log(1 - \alpha)$, one finds:

$$G(0, t) = \frac{1}{\log(1 - \alpha)} \log \left[\frac{(1 - \alpha)e^{(1-\alpha)t}}{e^{(1-\alpha)t} - \alpha} \right] \quad (10)$$

In this case, again $p(t) = \partial G(0, t)/\partial t \sim e^{-t/t^*}$ when $t \gg t^*$ whereas $p(t) \sim t^{-1}$ when $t \ll t^*$, which means that the critical exponent for the lifetime p.d.f is now -1 .

We now discuss, qualitatively first, the solution in the general case when all the coefficients are different from zero and $b_0 \sim d_0$, $b_1 \sim d_1$. Heuristically, long-living species have typically a large number of individuals. For such species the b_0 and d_0 terms can be reasonably neglected. Thus, one expects a crossover from the $t^{-3/2}$ to the t^{-2} behavior at a certain characteristic time and finally an exponential decay beyond another characteristic time t^* shown in Figure 1.

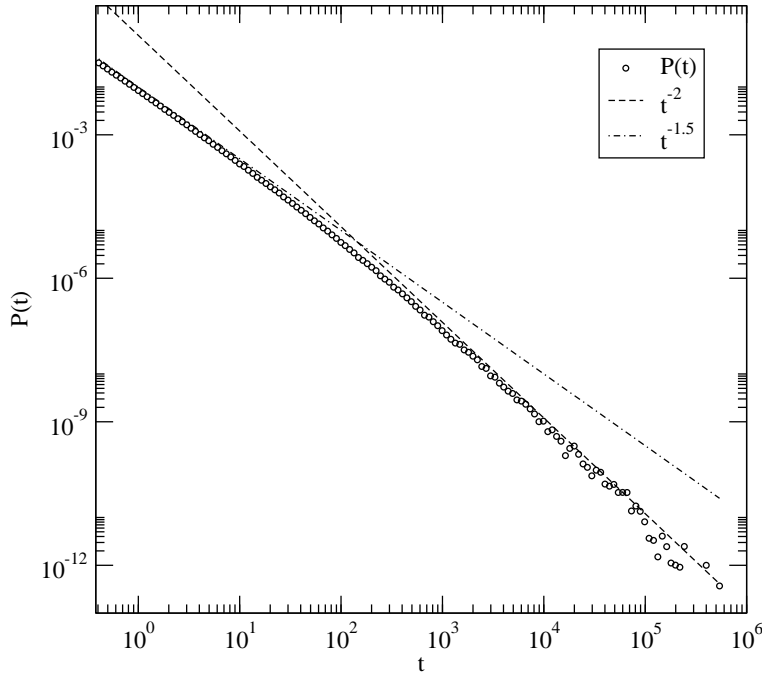


Figure 1: numerical sample of the lifetime probability distribution function with parameters $d_1 = 1$, $b_1 = 1 - 5 \cdot 10^{-5}$, $b_0 = d_0 = 10$. Notice the crossover between the two power-laws (shown in the picture, notice the log-log scale) and the beginning of the exponential regime.

In the Methods section, we provide the analytical solution of the general case, proving rigorously both the asymptotic critical behaviors and the scaling of the solution with the ratio b_0/b_1 . In the following, instead, we discuss the main results and their

consequences. In terms of the Laplace transform of $P_0(t)$, $\tilde{P}_0(s) = \int_0^\infty P_0(t)e^{-ts}$, the exact solution for the critical case $b_0 = d_0 = r$ and $b_1 = d_1 = 1$, is given by

$$s\tilde{P}_0(s) - 1 = -\frac{\int_1^\infty \frac{dy}{y} e^{-sy}(1 - \frac{1}{y})^r}{\int_1^\infty dy e^{-sy}(1 - \frac{1}{y})^r} = \frac{1}{\partial_s \log N(s, r)} \quad (11)$$

where we have defined $N(s, r) = \int_1^\infty \frac{dy}{y} e^{-sy}(1 - \frac{1}{y})^r$. For small s the function $N(s, r)$ diverges as $-c \log s$, where c depends only on r ; this implies that $\tilde{P}_0(s)$ behaves as $\tilde{P}_0(s) \sim \frac{1}{s} + c \log s$. The Tauberian theorem ensures in this case that $P_0(t)$ behaves like $1 - ct^{-1}$ for large t , implying that the lifetime distribution has a t^{-2} power-law tail.

In order to derive the crossover to the $t^{-3/2}$ behavior, we need to focus on time-scales $t \ll 1/r$ for $r \ll 1$. This is related to the limit $s \rightarrow 0$ with rs fixed in the solution, for which one obtains

$$N(s, r) = \int_0^\infty \frac{dx}{x} e^{-\sqrt{rs}(x + \frac{1}{x})} = 2K_0(2\sqrt{rs}) \quad (12)$$

where K_0 is a modified Bessel function. Using this result and Eq. (11) one gets that the lifetime distribution obeys the following scaling form:

$$p(t) = t^{-2} f\left(\frac{t}{r}\right) \quad (13)$$

where $f(x) \rightarrow \text{const}$ when $x \rightarrow \infty$, leading to the t^{-2} scaling at large t , and $f(x) \sim \sqrt{x}$ when $x \rightarrow 0$, corresponding to the random walk scaling $t^{-3/2}$ at intermediate t . The validity of this scaling law is numerically confirmed (see Fig.2).

Discussion

As sketched in the Introduction, the fact that species lifetimes are usually exponentially distributed is often referred to as Van Valen's law [18]: under the assumption that the fitness level is correlated in some way to the extinction probability, Van Valen states that an observed exponential lifetime distribution is the fingerprint of an acting Red Queen mechanism. Later, more detailed analysis (and datasets) [15]

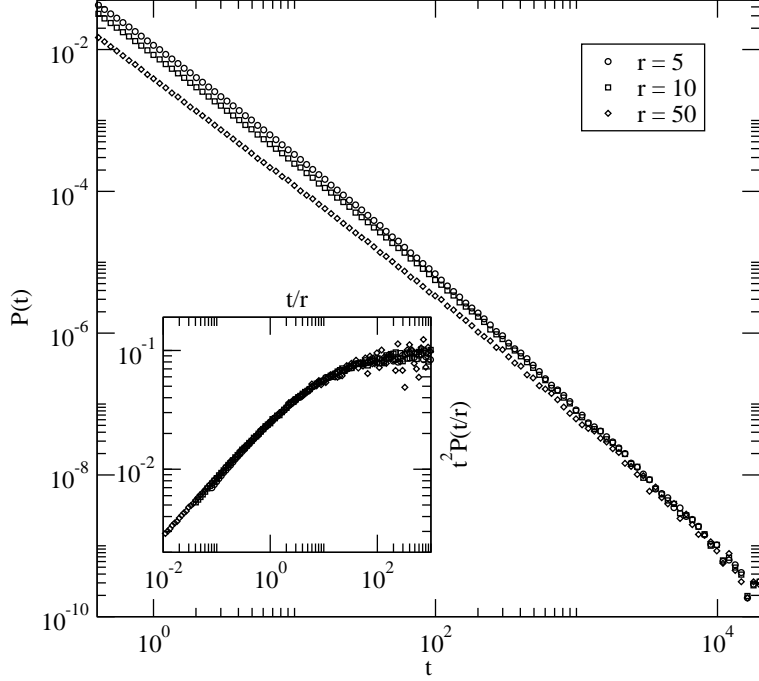


Figure 2: Plot of curves with different values of $b_0 = d_0 = r$, shown in the legend. The other parameters are $d_1 = 1$, $b_1 = 1 - 10^{-5}$. Collapse of the curves according to the scaling law (13) is shown in the inset.

brought to the observation of power-law behaviors in genera lifetimes, while species exponential lifetime distribution have been generally confirmed. This difference is, to a certain degree, counterintuitive as one would expect to see a deviation from criticality as a finite size effect when looking at long time scales. A possible explanation proposed in Refs. [11, 12] is that at longer timescales, like those relevant for genera extinction, collective events like mass extinctions play a more important role. The interdependence of generic taxa in an ecosystem generates stronger correlations in their probability to survive, and these correlations, in turn, may originate a power-law behavior in the lifetime distribution [11, 12].

We have shown that also in a simple model, in which every species undergoes an effective *independent* dynamics, a critical behavior for the lifetimes may occur, with an exponent which is compatible with the observed value. This critical behavior is generated only by demographic stochasticity, which is known to be a very important

factor in causing species extinction [36]. Interestingly enough, the hypothesis underlying this model are not so different to that bringing Van Valen to the explanation of the exponential species lifetime: our results clearly indicate that the presence of a Red Queen effect, i.e. the fitness equivalence of all species, do not ensure an exponential lifetime distribution, as far as one takes into account the population sizes in an explicit way. In some sense, in these models the population size acts as a simple “memory” of the evolutionary history of the species.

It is worthwhile to connect our approach with a model proposed by Raup [37] as a null model for the survivorship curves of Phanerozoic genera (the lifetime distribution can be thought as the derivative of the survivorship curve). This model, fitting rather well the fossils data, assumes that species constituting the genera have a constant speciation and extinction rate. Obviously, the resulting lifetimes distribution is the same that we recover as a limiting case of our model in Eq.(7): the only difference is that, in Raup’s case, the branching-like dynamics is applied at the level of species (not at the level of individuals). This implies that our model is well compatible with the data from the fossils record, with the advantage of being grounded on more realistic (and testable) hypothesis than the assumption of constant species immigration and speciation rates.

In our framework, it is also possible to explain why the critical behavior in the lifetimes is generally observed when studying higher taxonomic levels. Let us assume that we can neglect the terms b_0 and d_0 , as far as we are interested in the tail of the lifetime distribution. By taking the mean value of the distribution in Eq. (9), the typical population size can be expressed as:

$$\langle n \rangle = \frac{\alpha}{(\alpha - 1)} \frac{1}{\log(1 - \alpha)} \quad (14)$$

The r.h.s of Eq. (14) diverges when $\alpha \rightarrow 1^-$: thus, a choice of the parameters closer to criticality implies a larger population size. Since genera lump the individuals of many species, the effective value of α for a genera should be closer to 1 than it is for species. Therefore, it may not be possible to observe the power-law in the species lifetime due to the experimental error bars and the presence of the exponential cutoff occurring at $t \sim (1 - \alpha)^{-1}$ according to eq.(7) which, depending on its value, might mask both scaling regimes, i.e. $t^{-3/2}$ and t^{-2} or only the latter.

Finally, we demonstrated that, while 'local' birth and death terms, i.e. terms that are negligible in the large population size limit, are known to modify the mean species extinction time [38, 39], they are unable to affect the long timescale behavior of the lifetime distribution: the critical behavior of the distribution, in this class of models, is uniquely determined by the Galton-Watson part of the dynamics. Given the robustness of this 'criticality' with respect to modification of the dynamics on small scale, we suggest the hypothesis that the observed power law could be simply a consequence of the branching-like structure of single population dynamics, rather than an effect of the interactions among different species.

Methods

In these notes we outline the main steps of the derivation of the results. Let us firstly focus on the limit $b_0 = d_0 = 0$ when the process reduces to a Galton - Watson branching process. Without loss of generality, we can set $d_1 = 1$ and $b_1 = \alpha$ in what follows. Introducing the characteristic function

$$G(x, t) = \sum_{n=0}^{\infty} P_n(t) x^n, \quad (15)$$

the birth and death equation can be transformed in a first-order p.d.e. for $G(x, t)$

$$\partial_t G(x, t) = (\alpha x^2 + 1 - (\alpha + 1)x) \partial_x G(x, t). \quad (16)$$

This equation can be integrated using, for example, the characteristic method (see ref. 1). Taking as initial condition $G(x, 0) = x$, which corresponds to Eq. 4 in the main text, the complete solution is

$$G(x, t) = \frac{(1 - x) - (1 - \alpha x)e^{(1-\alpha)t}}{\alpha(1 - x) - (1 - \alpha x)e^{(1-\alpha)t}}, \quad (17)$$

from which we obtain

$$P(0, t) = G(0, t) = \frac{1 - e^{(1-\alpha)t}}{\alpha - e^{(1-\alpha)t}}, \quad (18)$$

and, taking the time derivative of this, we derive Eq. 7 of the main text. It is also easy to see that in the scaling limit, i.e. for $t^* = 1/(1 - \alpha) \gg 1$ and t/t^* fixed, $p(t)$ can be cast in the scaling form 8.

In order to deal with the general case, we make a Laplace transform with respect to time of the generating function and define

$$\tilde{G}(x, s) = \int_0^\infty dt e^{-st} G(x, t) = \int_0^\infty dt e^{-st} \sum_{n=0}^\infty P_n(t) x^n. \quad (19)$$

Then the equation of the dynamics becomes

$$\begin{aligned} & [\alpha x^2 + 1 - (\alpha + 1)x] \partial_x \tilde{G}(x, s) + \\ & + \left[b_0 x + \frac{d_0}{x} - b_0 - d_0 - s \right] [\tilde{G}(x, s) - g_0(s)] = s g_0(s) - x, \end{aligned} \quad (20)$$

where we defined $g_0(s) = \tilde{G}(0, s)$, which is the Laplace transform of $P_0(t)$, the function we wish to compute. Defining $F(x, s) = \tilde{G}(x, s) - g_0(s)$ and using the fact that $g_0(s)$ does not depend on x , we obtain the following equation for $F(x, s)$:

$$\partial_x F(x, s) + p(x, s) F(x, s) = q(x, s), \quad (21)$$

where

$$\begin{aligned} p(x, s) &= \left[\frac{d_0}{x} - \frac{b_0 - d_0 \alpha}{1 - \alpha x} - \frac{s}{(1 - \alpha x)(1 - x)} \right] \\ q(x, s) &= \frac{s g_0(s) - x}{(1 - \alpha x)(1 - x)}. \end{aligned} \quad (22)$$

Eq. **7** should be solved with the boundary conditions

$$F(1, s) = \frac{1}{s} - g_0(s) \quad (23)$$

$$F(0, s) = 0. \quad (24)$$

Due to the presence of singularities at $x = 0$ and $x = 1$, some care must be taken when imposing these conditions on the general solution of Eq. **7**. Our strategy is that of solving Eq. **7** with a modified initial condition (Eq. **9**) at $x = 1 - \epsilon$

$$F(1 - \epsilon, s) = \frac{1}{s} - g_0(s). \quad (25)$$

Then we will impose condition **10** on the resulting expression, which leaves us with an equation for $g_0(s)$. Finally, we shall restore the boundary condition **9** by taking the limit $\epsilon \rightarrow 0$. Such an ϵ -“regularization” procedure allows us to circumvent the problem of dealing with the singularities at $x = 1$ of Eq. **7**. Notice that, as long as $\alpha =$

$b_1 \leq 1 = d_1$, one has $\lim_{t \rightarrow \infty} P_0(t) = 1$, i.e. the probability of being asymptotically extinct approaches 1.

The generic form of the solution of Eq. 7 with boundary condition 11 is

$$F(x, s) = e^{\int_x^{1-\epsilon} dx' p(x', s)} \left[\frac{1}{s} - g_0(s) \right] - \int_x^{1-\epsilon} dx' q(x', s) e^{\int_x^{x'} dx' p(x', s)}. \quad (26)$$

The resulting expression is rather complex and it will be considered later on. We shall first specialize to the particular case $b_0 = d_0 = r$ and $\alpha = 1$ discussed in the main text, which describes the crossover between the two power law regimes, and then the sub-critical case $\alpha < 1$.

For $b_0 = d_0 = r$ and $\alpha = 1$, the coefficients take the simpler form

$$\begin{aligned} p(x, s) &= \frac{r}{x} - \frac{s}{(1-x)^2} \\ q(x, s) &= \frac{sg_0(s) - x}{(1-x)^2}. \end{aligned} \quad (27)$$

Up to the leading order in ϵ , the solution is

$$F(x, s) = \frac{e^{-\frac{s}{\epsilon}} (g_0(s) - \frac{1}{s}) - \int_x^{1-\epsilon} dt \frac{sg_0(s) - t}{(1-t)^2} t^r e^{-\frac{s}{1-t}}}{x^r e^{-\frac{s}{1-x}}}. \quad (28)$$

Since the denominator diverges when $x \rightarrow 0$, in order to have $F(0, s) = 0$, we have to impose that the numerator should be equal to zero. After taking the limit $\epsilon \rightarrow 0$, this yields an equation for $g_0(s)$, which reads

$$\int_1^x dt \frac{sg_0(s) - t}{(1-t)^2} t^r e^{-\frac{s}{1-t}} = 0. \quad (29)$$

Finally, upon making the substitution $\frac{1}{1-t} = y$ and rearranging terms, we arrive at our main result, Eq. 11 of the main text with $N(s, r)$ given by

$$N(s, r) = \int_1^\infty \frac{dy}{y} e^{-sy} \left(1 - \frac{1}{y}\right)^r. \quad (30)$$

For r fixed and $s \ll 1$, the integral in $N(s, r)$ is dominated by the region $y \sim 1/s$ and hence $N(s, r) \sim -\log s$; the application of the Tauberian theorem (see ref. 2) finally demonstrate the t^{-2} asymptotic behavior of the lifetimes. In order to derive

Eq. **12** of the paper, in the limit $s \ll 1$ with rs fixed, we make the change of variables $x = \sqrt{\frac{s}{r}}y$ in Eq. **16**, exponentiate the term $(1 - 1/y)^r$ in the integral and make a power expansion

$$N(s, r) = \int_{\sqrt{\frac{s}{r}}}^{\infty} \frac{dx}{x} e^{-\sqrt{rs}(x + \frac{1}{x} - \sqrt{\frac{s}{r}}\frac{1}{x^2} + \dots)}, \quad (31)$$

which, neglecting corrections of order $\sqrt{s/r}$ leads to Eq. **12** of the main text. When $rs \gg 1$, i.e. for $t \ll r \gg 1$, we can use the asymptotic expansion for the modified Bessel function, K_0 (see Eq. **12** of the main text) or, more directly, we can estimate the integral with the saddle point method: the maximum of the argument of the exponential occurs at $x^* = 1$ and, expanding it to second order around $x^* = 1$, we find

$$N(s, r) \approx e^{-2\sqrt{rs}} \int_{\sqrt{\frac{s}{r}}}^{\infty} dx e^{-\sqrt{rs}(x-1)^2} \approx e^{-2\sqrt{rs}} (rs)^{-\frac{1}{4}}. \quad (32)$$

Hence

$$sg_0(s) - 1 = \frac{1}{\partial_s \log N(s, r)} = -\frac{1}{\sqrt{\frac{r}{s}} + \frac{1}{4s}}, \quad (33)$$

which means that for $s \rightarrow 0$, $sg_0(s) - 1 \sim -\sqrt{s}$ corresponding, according to the Tauberian theorem, to the random walk behavior $P_0(t) \sim 1/\sqrt{t}$. The fact that the scaling variable in the derivation above is rs , implies that the crossover time should be proportional to r . Indeed using Eqs. **11** and **12** of the main text and the inverse Laplace transform one derives the scaling form

$$p(t) = \frac{1}{t^2} f\left(\frac{t}{r}\right), \quad (34)$$

where the function $f(x) \sim \sqrt{x}$ for small value of the argument (i.e. when $x \ll 1$) and approaches a constant when x becomes large.

Finally, let us discuss the sub-critical case $b_1 < d_1$. Using exactly the same strategy as for the critical case, we find that the condition $F(0, s) = 0$ leaves us with the following equation:

$$\int_0^1 dt t^{d_0} (1 - \alpha t)^{b_0/\alpha - d_0 - s/(1-\alpha) - 1} (1 - t)^{1/(1-\alpha) - 1} (sg_0(s) - t) = 0. \quad (35)$$

Now, we substitute $y = 1 - t$ and solve for $g_0(s)$

$$sg_0(s) - 1 = -\frac{\int_0^1 dy (1 - y)^{d_0} [1 - \alpha(1 - y)]^{b_0/\alpha - d_0 - s/(1-\alpha) - 1} y^{s/(1-\alpha)}}{\int_0^1 dy (1 - y)^{d_0} [1 - \alpha(1 - y)]^{b_0/\alpha - d_0 - s/(1-\alpha) - 1} y^{s/(1-\alpha) - 1}}. \quad (36)$$

The integral on the numerator is finite when $s \rightarrow 0$, whereas that on the denominator has a leading singularity of order $(1 - \alpha)/s$. This implies that $sg_0(s) \simeq -A/[1 + st^*]$, with A constant and $t^* \sim 1/(1 - \alpha)$, which is exactly the Laplace transform of a distribution of the form

$$p(t) \simeq e^{-t/t^*}.$$

This confirms both the asymptotic exponential decay of $p(t)$ and the scaling of the cutoff time $t^* \sim 1/(1 - \alpha)$.

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